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Farmlands with smaller crop fields have higher within-field biodiversity

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ABSTRACT

Simple rules for landscape management seem elusive because different species and species groups are associated with different land cover types; a change in landscape structure that increases diversity of one group may reduce diversity of another. On the other hand, if simple landscape–biodiversity relationships do exist despite this complexity, they would have great practical benefit to conservation management. With these considerations in mind, we tested for consistent relationships between landscape heterogeneity and biodiversity in farmland (the cropped areas in agricultural landscapes), with a view to developing simple rules for landscape management that could increase biodiversity within farmland. Our measures of farmland heterogeneity were crop diversity and mean crop field size, where increases in crop diversity and/or decreases in mean field size represent increasing landscape heterogeneity. We sampled the abundance, and alpha, gamma and beta diversity of birds, plants, butterflies, syrphids, bees, carabids and spiders, in crop fields within each of 93 1 km × 1 km agricultural landscapes. The landscapes were selected to represent three gradients in landscape composition and heterogeneity: proportion of the landscape in crop, mean crop field size and Shannon crop type diversity of the farmland. We found that mean crop field size had the strongest overall effect on biodiversity measures in crop fields, and this effect was consistently negative. Based on our results we suggest that, if biodiversity conservation in crop fields is a priority, policies and guidelines aimed at reducing crop field sizes should be considered.

1. Introduction

Landscape management is critical for biodiversity conservation (Lindenmayer et al., 2008; Tscharntke et al., 2012). However, landscape management is hindered by an inherent conundrum: different species and species groups are associated with different land cover types, so a landscape that increases diversity of one species group may reduce diversity of another, leading to low cross-taxa congruence of species diversity across sites (Hess et al., 2006; Wolters et al., 2006; Gagné and Fahrig, 2011). Since a given landscape can be structured in only one way, we must address the question, is it possible to manage landscapes to simultaneously benefit different species and species groups with different land cover associations?

One potential solution to this dilemma is to encourage landscape management policies that increase landscape heterogeneity, without necessarily delving into particular species habitat relationships (*e.g.* Montigny and MacLean, 2005; Kati et al., 2010; Lindsay et al., 2013). Landscape heterogeneity has two distinct components; compositional heterogeneity is higher when there are more land cover types and when these are more evenly represented in the landscape, and configurational heterogeneity refers to the degree of spatial complexity of the landscape pattern, irrespective of the cover types present (Duelli, 1997; Fahrig and

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Nuttle, 2005). There are reasons to expect positive effects of both components of heterogeneity on biodiversity (reviewed in Fahrig et al., 2011). A diversity of cover types (compositional heterogeneity) should provide habitat and resources for a larger variety of species, and when these different cover types are more interspersed with each other (configurational heterogeneity), species that use more than one cover type should benefit through 'landscape complementation' (*sensu* Dunning et al., 1992; *e.g.* Pope and Fahrig, 2000; Ethier and Fahrig, 2011).

Despite these arguments, actually managing for landscape heterogeneity is still constrained by two species-specific considerations. First, any description of landscape heterogeneity requires a decision on thematic resolution of the landscape map: which and how many different land cover types, *e.g.* forest types, crop types, or wetland types, should be identified as separate cover types? Ultimately the answer to this question should depend again on the particular species or species group, each of which responds to a different set of cover types in the landscape, resulting in different measures of 'functional heterogeneity' (*sensu* Fahrig et al., 2011). The second species issue results from the 'area-heterogeneity trade-off' or the 'intermediate heterogeneity hypothesis' (Kadmon and Allouche, 2007; Fahrig et al., 2011), which argues that, within a fixed area, increasing compositional heterogeneity by increasing the number of cover types simultaneously reduces the area of each individual cover type. This should lead to a peaked biodiversity–heterogeneity relationship, since landscapes with very high heterogeneity will not contain enough of most cover types to maintain viable populations of the species associated with those cover types. Where on the heterogeneity axis this peak occurs should depend not only on the particular measure of heterogeneity but also on the particular suite of species considered (Allouche et al., 2012).

Thus, development of simple rules for landscape management seems elusive due to the inherent complexities associated with species-contingent responses to landscape pattern. On the other hand, if simple landscape–biodiversity relationships do exist despite these complexities and contingencies, they would have great practical benefit to conservation management. With these considerations in mind, we tested for consistent relationships between landscape heterogeneity and biodiversity in farmland (the cropped areas in agricultural landscapes), with a view to developing simple rules for management that could increase biodiversity within farmland. We chose farmland specifically because the spatial patterning of farmland is largely under human control, and therefore susceptible to landscape management policies.

Over the past half-century, agricultural intensification has led to reduced biodiversity in farmed landscapes (Geiger et al., 2010; Flore et al., 2011; Kirk et al., 2011; Armengot et al., 2012). In fact, globally, about 60% of red-listed amphibians and birds, and between 10 and 20% of other red-listed taxa are threatened by intensive agriculture (Norris, 2008). Along with increased application of agri-chemicals, agricultural intensification has entailed important landscape changes. More intensive landscapes contain fewer crop types, grown in larger fields, than less intensive landscapes (Kareiva et al., 2007). In other words, agricultural intensification is reducing both the compositional heterogeneity and the configurational heterogeneity of farmlands.

The impact of this reduction in heterogeneity on farmland biodiversity is poorly understood, because most studies to date were not designed to estimate its effects on biodiversity specifically within the crop fields (*e.g.* Freemark and Kirk, 2001; Williams and Kremen, 2007; Doxa et al., 2010; Poggio et al., 2010; Smith et al., 2010; Smukler et al., 2010; Poveda et al., 2012; Power et al., 2012; Woltz et al., 2012; Lindsay et al., 2013). Given the growing need for food and the dominance of farmland in many parts of the world, it is important to consider the biodiversity represented in the farmed areas (crop fields) of agricultural landscapes, and whether this biodiversity can be augmented through policies aimed at changing the pattern of farmland. If a significant component of the effect of agricultural intensification on farmland biodiversity is due to reduced farmland heterogeneity, then perhaps policies and guidelines could be developed to augment farmland biodiversity by increasing farmland heterogeneity.

Our overall objective is to determine whether there are consistent patterns relating farmland heterogeneity to farmland species diversity. Does the diversity of widely differing species groups within crop fields vary in a consistent way with varying farmland heterogeneity? We consider the two types of heterogeneity, compositional and configurational heterogeneity, independently. A farmland with high compositional heterogeneity has many crop types (crop richness) and/or similar areal coverage of the crop types within it (crop evenness), and a farmland with higher configurational heterogeneity has smaller crop fields and a greater total length of field edges. Although both components of heterogeneity may positively affect biodiversity, the relative strength of their effects could be quite different, and this would have important implications for landscape management aimed at increasing biodiversity within crop fields. In particular, if biodiversity does show consistent responses to farmland heterogeneity across species groups, would it be more effective to implement policies that encourage a higher diversity of crop types, or that encourage reductions in crop field sizes?

2. Material and methods

2.1. Overview

We sampled biodiversity in crop fields within 93 1 km × 1 km agricultural landscapes, across an area of about 10,000 km^2 (1 million ha) in Eastern Ontario, Canada (Fig. 1). Agricultural land use dominates the area and is characterized by maize (21%), soybean (19%), forage crops (alfalfa, clover, hay; 30%), and wheat (3%) (Ontario Ministry of Agriculture and Food, 2011). We chose 1 km^2 sample landscapes because this is approximately the mean size of farms in the region, so it is a relevant scale for landscape management. Note, however, that the boundaries of our sample landscapes did not coincide with individual farms. The landscapes were selected to represent three gradients in landscape composition and heterogeneity – proportion of the landscape in crops (where 'crop' includes annual row crops and perennial crops such as hay), Shannon crop type diversity, and mean crop field size.

We surveyed biodiversity in the farmland (cropped) portions of the landscapes. This included mean alpha diversity, gamma diversity, beta diversity, and relative abundance per landscape, of seven species groups: birds, plants, butterflies, syrphids, bees, carabids, and spiders. These groups were selected (i) to capture a range of potential responses to landscape pattern, (ii) to represent a range of ecosystem services (cultural, supporting, pollination, and pest control), and (iii) for relative ease of sampling, given the scale of the project. Data acquisition was a large undertaking. The major components (details below) were: geomatics-based analyses for initial landscape quantification and selection, obtaining permission from and maintaining communications with 253 private land owners on whose properties we conducted the biodiversity sampling, field surveys of seven species groups, within- and post-season geomatics-related work and field validation to obtain detailed maps and derived landscape variables, and identification of arthropods returned to the lab. The work involved 27 people. Forty-six landscapes were surveyed in 2011, followed by an additional 47 landscapes in 2012.

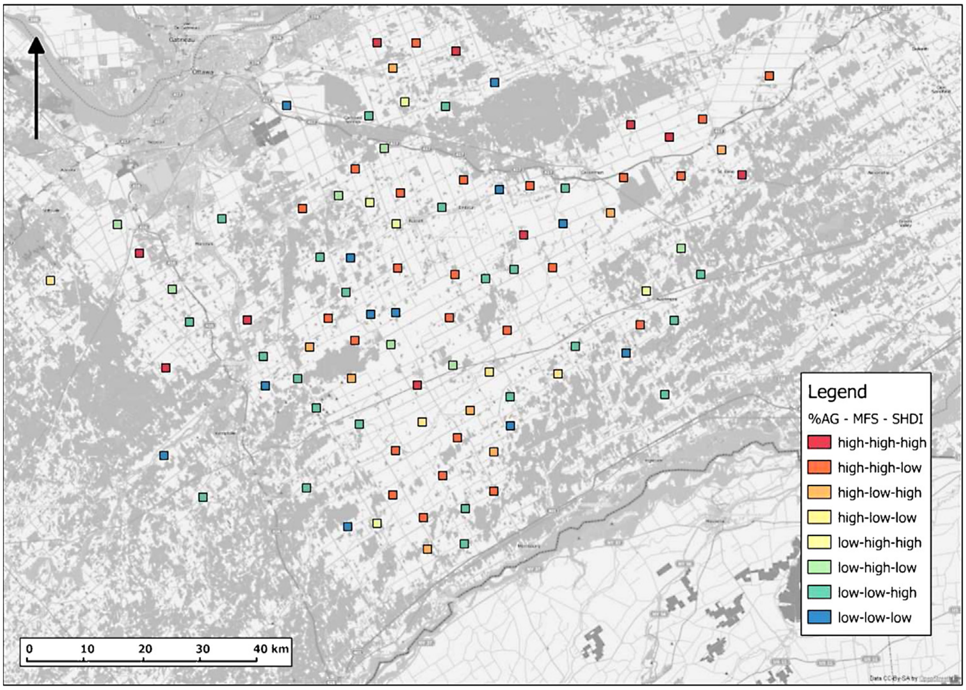

Fig. 1. Ninety-three 1 km^2 sampled landscapes within eastern Ontario, Canada. For presentation purposes, we binned the values of each of the three landscape variables – proportion of the landscape in crops (%AG), mean crop field size (MFS), and Shannon diversity of crop types within farmland (SHDI) – into low and high values; different colours represent the eight combinations of low and high values of each of the three landscape variables. Note that these are actually continuous variables, and were analyzed as such.

2.2. Landscape selection and quantification

Details of the landscape selection process are in Pasher et al. (2013). The overall objectives of the landscape selection process were to select agricultural landscapes that (i) were far enough apart to ensure spatial independence (a minimum centre to centre distance of 3.5 km); (ii) represented as large as possible ranges of values of the landscape heterogeneity variables (Shannon diversity of crops and mean crop field size) across landscapes; (iii) had low cross-landscape correlation between the heterogeneity variables and also between the heterogeneity variables and the amount of crop cover in the landscape; and (iv) avoided regional trends in the heterogeneity variables. The landscape selection process was based on a land cover map of major crop types derived from multiple within-growing-season Landsat-5 satellite images (30 m pixels) obtained in 2007, with an overall accuracy of 81% based on ground reference data collected in 2007. Crop fields were delineated using panchromatic SPOT satellite imagery (10 m pixels) from 2007, which were then up-sampled to 30 m pixels to remain comparable with the Landsat-5 imagery (Pasher et al., 2013).

While the resulting land cover map was adequate for landscape selection, given the data available prior to biodiversity sampling, its spatial resolution (30 m pixels) was coarser than optimal for accurate delineation of field boundaries and identification of narrow strips of non-crop covers. In addition, due to crop rotation and field enlargement, there were differences in land cover between 2007 when the satellite imagery were taken, and our sampling years, 2011 and 2012. Therefore, we commissioned aerial photography (40 cm pixels) of our sample landscapes during the seasons in which we conducted the biodiversity sampling. We used these photos to create detailed land cover maps of each 1 km × 1 km landscape at 40-cm resolution. These maps were validated by field crews during each field season (*e.g.* Fig. 2). Separate crop fields were delineated based on either visible field boundaries or a change in crop type or both. Therefore, areas of the same crop type that were separated by a non-crop field boundary were considered separate fields, and areas of different crop types that were not separated by a non-crop boundary were also considered separate fields. From these detailed land cover maps in the year of sampling, we then calculated for each landscape three landscape variables: proportion of the whole 1 km^2 landscape in crops, mean size of all crop fields in the landscape, and Shannon diversity of crop types within the farmland portion of the landscape.

2.3. Biodiversity surveys

Within each landscape, we initially chose four sites at field boundaries between two crop fields, such that sites were at least 200 m apart, at least 50 m from non-crop areas (*e.g.* forests, wetlands, abandoned fields, farmsteads, roads), and at least 50 m from the edge of the sample landscape. Within these constraints we selected field boundaries containing as little tree and shrub cover as possible; 76% of selected sites had less than 66% cover of trees or shrubs along their length. Bird surveys were conducted at these four sites, encompassing observations in both adjacent crop fields. Plant surveys were conducted in one of the two adjacent crop fields (chosen at random) at each of the four sites. Invertebrate taxa were surveyed in three of these four crop fields (selected at random). To avoid potential correlations between landscape variables and sampling date, the sequence in which landscapes were sampled was randomized for all surveys. Farming activities resulted in temporary inaccessibility of some landscapes, such that the actual number of landscapes studied per species group were: birds, 92; plants, 93; butterflies and syrphids, 91; bees, 46 (2011 only); carabids and spiders, 92.

2.3.1. Birds

Birds were surveyed using 10-min point counts, between sunrise and four hours after sunrise between 24 May and 9 July in

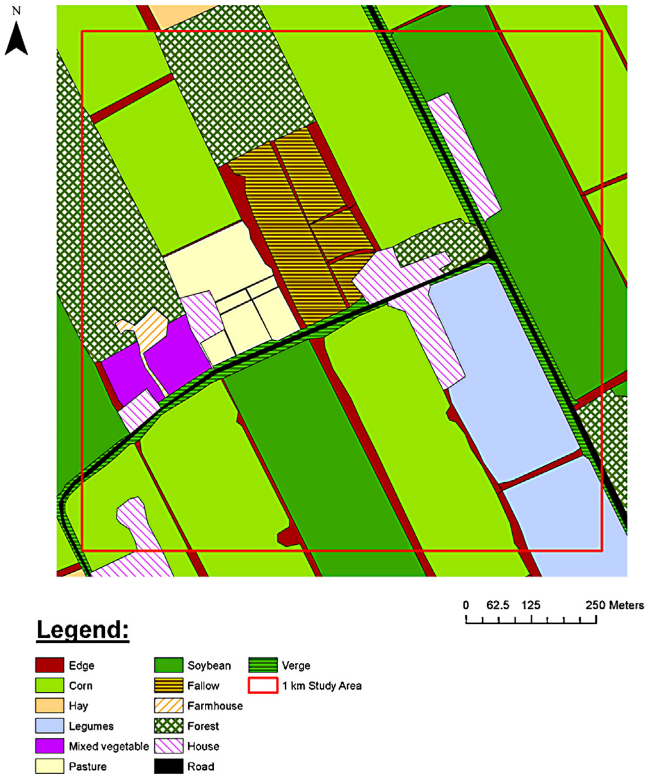

Fig. 2. Example land cover map of one of 93 sampled 1 km^2 landscapes, showing detailed classification based on ground validation and air photography taken during the sample season.

both years. One point count was conducted at each of the four sites in each landscape. Point counts were not conducted when winds reached Beaufort scale 3 or higher, or during precipitation or fog. Point counts were conducted by three observers, who were randomly assigned to landscapes (one observer worked in both 2011 and 2012, the other two in one year each). Only birds observed within 50 m of the observer were included in the analyses here. Detectability of birds in open habitats within 50 m of the observer is typically very high (Reynolds et al., 1980; Shustack et al., 2010). Given the sample site selection process (as described above), the 50-m radius circles surveyed for birds were as similar as possible, *i.e.* each contained about 0.4 ha of each of two crop fields and 100 m of a field boundary. This minimized variation in detectability among sites. In addition, randomization of date and observer across landscapes ensured that any variability in detectability did not bias our results. We therefore used the point count data as estimates of relative bird abundance and diversity.

2.3.2. Plants

At each of the four sites per landscape, one of the two crop fields was selected at random, and plants were counted along a 50 m transect placed parallel to the field boundary, about 25 m into the crop. The surveyor recorded all plant species present within 1 m on either side of the transect. Surveys were conducted twice, between 24 May and 9 July and again between 17 July and 30 August in both years, and the species lists from the two surveys at each site were combined.

2.3.3. Butterflies

Butterflies were surveyed by walking the 50-m plant transect (above) at a rate of 5 m per min, and recording all butterflies seen within an imaginary 5 m^3 box (*i.e.* within 5 m from the ground, 2.5 m to each side of the transect, and 5 m in front of the observer), as the observer moved. Any butterfly not immediately identifiable was captured for closer examination and the clock was stopped during this time, so that time spent identifying butterflies was not included in the 10-min transect walk. Individual butterflies were counted only once. Butterfly surveys were conducted twice, first between 27 June and 3 August and again between 4 and 31 August in both years. Surveys at the same site were at least 12 days apart. Abundance and species lists were summed over the two surveys at each site.

2.3.4. Syrphids

Syrphid surveys were conducted immediately following the butterfly surveys along the same transects, moving at the same speed. Any syrphid observed within an imaginary 2 m^3 box in front of the observer (the distance that observers could reach with a net) was captured with a butterfly net (38 cm diameter). The timer was stopped while syrphids were processed, so that the total time spent actively observing syrphids was 10 min per transect. Syrphids were killed and preserved by placing them in a jar containing a layer of plaster of paris soaked with approximately 10 ml of ethyl acetate. They were returned to the lab, placed in a dry vial in the freezer, and later pinned and identified to species based on Vockeroth and Thompson (1987),Curran and Fluke (1926), Shannon (1926), Curran (1951), Telford (1970) and Vockeroth (1992). Abundance and species lists were summed over the two surveys at each site.

2.3.5. Bees

At each of the three sites in each landscape in 2011, six pan traps (coloured plastic cups) were placed on the tops of three poles, two traps per pole, with the poles placed at the two ends and the centre of the plant transect. We used three colours of pan traps (two pans of each colour at each site) – white, yellow and blue –, and each pole had two different colours. Traps were 2/3 filled with water, and dish soap was added at a rate of 10 drops per litre to break the surface tension. The poles were designed such that the height was adjustable. Pole height was set such that the pan openings were even with the top of the surrounding vegetation, allowing approaching bees to see them. The pans were in place for two periods of four days each, using the same random order of landscapes as for the butterfly and syrphid surveys; the first four-day period was between 27 June and 3 August and the second was between 4 and 31 August 2011. Once returned to the lab, samples were put in 70% ethyl alcohol and stored in the dark. The bees were later prepared (dried, fluffed, and pinned) and sent to specialists at Agriculture Canada and the American Museum of Natural History for identification. Abundance and species lists were summed over the two surveys at each site.

2.3.6. Carabids and spiders

Carabids and spiders were surveyed using pitfall traps, at the same three sites per landscape as above. Trapping was carried out for two periods of four days each at each landscape; the first four-day period was between 15 June and 14 July and the second was between 25 July and 31 August in both years. A pitfall trap was placed in the ground at each end of each plant transect, such that the top edge of the trap was level with the ground. Traps were 15 cm high with a 9-cm diameter opening, and were half-filled with water and dish soap was added at a rate of 10 drops per litre. A lid (approximately 20 cm^2) was place over each trap, approximately 3 cm above the ground, to protect the trap from rain. The trap contents were returned to the lab, where the carabids and spiders were washed, stored in 70% ethyl alcohol, and later identified to species. Ground beetle taxonomy followed Lindroth (1961, 1963, 1966, 1968, 1969) and spider taxonomy followed Ubick et al. (2005). Abundance and species lists for each group were summed over the two surveys at each site.

2.4. Analyses

We calculated mean alpha diversity for each taxon in each landscape, as the mean number of species per sample site (*i.e.* across four sites per landscape for birds and plants and across three sites per landscape for invertebrates). Gamma diversity for each taxon in each landscape was the total number of species identified across all the sampled sites in the landscape. Beta diversity was the difference between gamma diversity and mean alpha diversity (Crist et al., 2003). In addition, for all taxa except plants we recorded the total number of individuals observed across all sample points in each landscape, which we called 'abundance'. Due to positive skew in the distribution of mean field size values across the sample landscapes, we used log mean field size in all analyses. The other predictors, proportion of the landscape in crops and Shannon diversity of crops, were well distributed across their ranges, with no skew.

We first corrected each response variable for the mean difference between years of sampling (2011 or 2012), by subtracting the difference from the values for the year with the larger mean, to control for potential year effects on biodiversity responses. We then logged all response variables to correct positive skew in the non-logged distributions, which was particularly apparent in the abundance data. Box plots of the logged variables are in Appendix 1.

To determine the direction and relative importance of the three landscape variables on each biodiversity response variable, we used a multi-model inference approach (Burnham and Anderson, 2002) to calculate and compare model-weighted mean coefficients. For each logged response variable we estimated all seven possible linear models, representing all possible combinations of the three landscape variables. We used linear regression with normal error distributions because the plotted relationships between predictors and logged responses appeared linear within the range of the predictors in our study area, the logged response variable distributions were not strongly skewed (Appendix 1), the distributions of residuals did not appear heteroscedastic, and we were not extrapolating our results beyond the measured range of our predictors. To estimate the relative effects of the three landscape variables for each biodiversity response variable, we compared the AICc model-weighted mean standardized coefficients. To calculate a model-weighted mean standardized coefficient for a given predictor, the standardized coefficient value from each model containing that predictor – here, each predictor was in 4 of the 7 models – is multiplied by the model weight (or support), calculated from the model AICc values. These values were then averaged, to give the model-weighted mean standardized coefficients (*i.e.* $\hat{\bar{\beta}}_j$, *sensu* Burnham and Anderson, 2002, p.152), which provide an estimate of the relative importance of the predictor variables (Smith et al., 2009). Finally, to answer our research question – are landscape effects consistent across biodiversity measures? – we qualitatively compared the direction and magnitudes of the model-weighted mean coefficients, across biodiversity measures. Analyses were conducted in R (R Core Team, 2013).

3. Results

Altogether we recorded 52 species of birds, 227 species of plants, 30 species of butterflies, 40 species of syrphids, 58 species of bees, 80 species of carabids, and 98 species of spiders (Appendix 2). The Pearson correlations between the landscape predictors were 0.67 for percent landscape in crops *vs*. log mean field size, −0.14 for percent landscape in crops *vs*. Shannon crop diversity, and −0.44 for log mean field size *vs*. Shannon crop diversity. Correlations among biodiversity measures were generally high within taxa, with the exception of correlations between abundance and diversity measures (Table 1A). Correlations between taxa were generally low (Table 1B).

The relative mean model-weighted standardized coefficients are shown in Fig. 3. Responses to percent of the landscape in crops were inconsistent across taxa (some negative, some positive) and generally weak. Responses to log mean crop field size were consistently negative across all taxa and response variables, with the exception of carabid abundance, and in most cases the effect of log mean crop field size was strongest of the three landscape variables. Responses to crop Shannon diversity were variable and very weak for all taxa. Plots of gamma diversity *vs*. log mean field size for all 7 taxa are in Fig. 4.

4. Discussion

Our most important finding is that increasing configurational heterogeneity of the cropped area, measured here as decreasing mean crop field size, has a consistent positive effect on biodiversity within farmland, *i.e.* within the cropped part of the landscape. This effect was consistent across taxa and across biodiversity measures. The one exception was carabid abundance, but *post hoc* analysis revealed that the positive response of carabid abundance was due to a positive response by the single most abundant carabid species, *Pterostichus melanarius*, an introduced species associated with cultivated land (Lindroth, 1966). When this species was removed, the response of carabid abundance to mean crop field size became negative (results not shown).

We emphasize that the positive effect of decreasing mean crop field size is not due to an increase in cover of natural and semi-natural areas in landscapes with smaller crop fields. Across our sample landscapes the correlation between the proportion of the landscape in crop and the proportion of the landscape in natural and semi-natural covers was −0.81, making these variables largely redundant. Therefore, by including the proportion of the landscape in crops in our models, we effectively controlled for the amount of natural and semi-natural cover on biodiversity responses when evaluating the effects of farmland heterogeneity. Our results suggest that, for a given amount of natural or semi-natural cover, farmlands with smaller crop fields have higher biodiversity.

What is the cause of this consistent relationship? We hypothesize that species in landscapes with small crop fields benefit from easy access to field boundary habitats (Merckx et al., 2009). As previously mentioned, we controlled for the total non-crop area in the landscapes. However, for a given amount of natural or semi-natural cover, farmlands with smaller crop fields have a higher proportion of their semi-natural cover as field boundaries than do farmlands with larger crop fields (Fig. 5). The results suggest that biodiversity in crop fields depends more strongly on the presence of semi-natural field boundary habitats than on larger natural areas such as forest patches. The importance of field boundaries to biodiversity within crop fields has been shown for many species groups including birds (reviewed in Vickery et al., 2009), invertebrates (Holland and Fahrig, 2000; Merckx et al., 2012; but see Werling and Gratton, 2008) and plants (Cordeau et al., 2012; Concepción et al., 2012a, b).

It is interesting to note that the consistent negative effect of mean crop field size across seven taxa occurred despite low cross-taxa correlations in biodiversity measures (Table 2). This implies that mean field size is not the main determinant of

Table 1
Correlations among response variables. Correlations within taxa (A) are generally high, while correlations between taxa (B) are generally low.

A Correlations within taxa

	Bird α	**Bird γ**	**Bird β**
Bird γ	0.88		
Bird β	0.72	0.96	
Bird abundance	0.77	0.68	0.56

	Plant α	**Plant γ**
Plant γ	0.96	
Plant β	0.89	0.98

	Butterfly α	**Butterfly γ**	**Butterfly β**
Butterfly γ	0.94		
Butterfly β	0.79	0.96	
Butterfly abundance	0.83	0.72	0.56

	Syrphid α	**Syrphid γ**	**Syrphid β**
Syrphid γ	0.95		
Syrphid β	0.85	0.97	
Syrphid abundance	0.75	0.75	0.69

	Bee α	**Bee γ**	**Bee β**
Bee γ	0.88		
Bee β	0.65	0.93	
Bee abundance	0.39	0.22	0.05

	Carabid α	**Carabid γ**	**Carabid β**
Carabid γ	0.90		
Carabid β	0.73	0.96	
Carabid abundance	0.16	0.06	−0.02

	Spider α	**Spider γ**	**Spider β**
Spider γ	0.94		
Spider β	0.80	0.96	
Spider abundance	0.84	0.78	0.66

B Correlations between taxa

	Bird α	**Plant α**	**Butterfly α**	**Syrphid α**	**Bee α**	**Carabid α**
Plant α	0.17					
Butterfly α	0.20	0.43				
Syrphid α	0.12	0.42	0.25			
Bee α	0.16	0.06	0.37	0.25		
Carabid α	−0.03	0.19	0.33	0.26	0.20	
Spider α	0.10	0.60	0.41	0.27	−0.01	0.07

	Bird γ	**Plant γ**	**Butterfly γ**	**Syrphid γ**	**Bee γ**	**Carabid γ**
Plant γ	0.15					
Butterfly γ	0.12	0.34				
Syrphid γ	0.01	0.41	0.17			
Bee γ	0.29	0.16	0.25	0.33		
Carabid γ	−0.01	0.32	0.41	0.29	0.07	
Spider γ	0.07	0.56	0.42	0.33	0.07	0.26

	Bird β	**Plant β**	**Butterfly β**	**Syrphid β**	**Bee β**	**Carabid β**
Plant β	0.12					
Butterfly β	0.06	0.27				
Syrphid β	−0.10	0.37	0.13			
Bee β	0.27	0.17	0.07	0.31		
Carabid β	0.02	0.35	0.42	0.28	−0.03	
Spider β	0.05	0.48	0.38	0.34	0.18	0.40

	Bird abundance	**Butterfly abundance**	**Syrphid abundance**	**Bee abundance**	**Carabid abundance**
Butterfly abundance	0.08				
Syrphid abundance	0.01	0.20			
Bee abundance	−0.20	0.07	−0.09		
Carabid abundance	−0.24	−0.05	0.06	0.00	
Spider abundance	0.00	0.36	0.22	−0.22	−0.12

biodiversity for most of the species groups; many other biotic and abiotic variables influence biodiversity, and these almost certainly differ among taxa. The relatively small role of landscape pattern can also be seen in the generally weak fit of the relationships (Fig. 4).

However, we also note that the influence of landscape pattern could be stronger than evidenced in our data. Due to our spatially and taxonomically extensive sampling (93 landscapes, 7 taxa), we sampled a relatively small number of sites (3–4 depending on taxon) within each landscape. Our biodiversity measures are

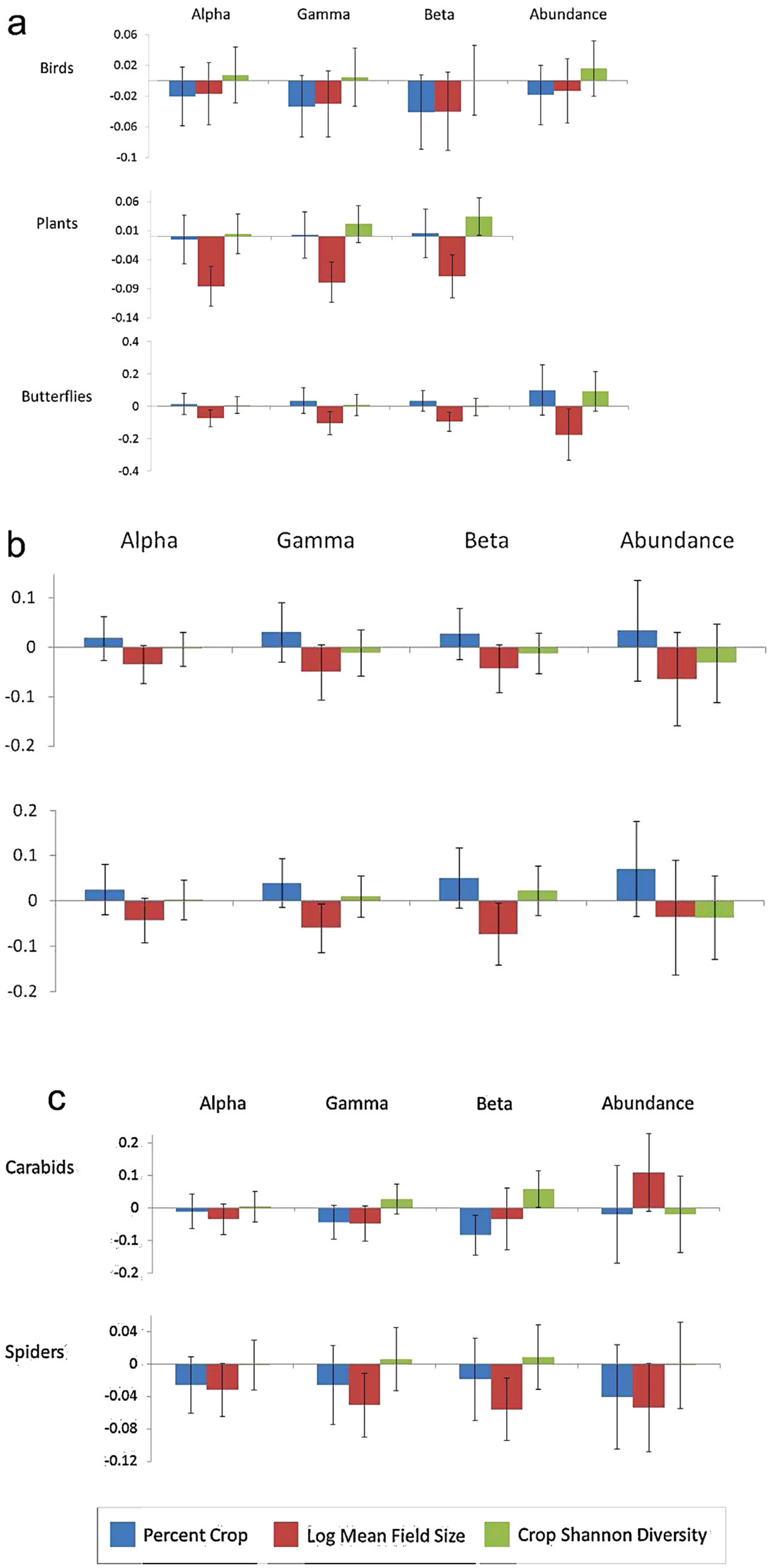

Fig. 3. Model-weighted mean standardized coefficients, from all seven models, for each logged response variable, with 95% confidence intervals. See Section 2 for explanation of model-weighted mean coefficients. Log mean crop field size has the largest effect in most cases and its effect is consistently negative across all responses except carabid abundance.

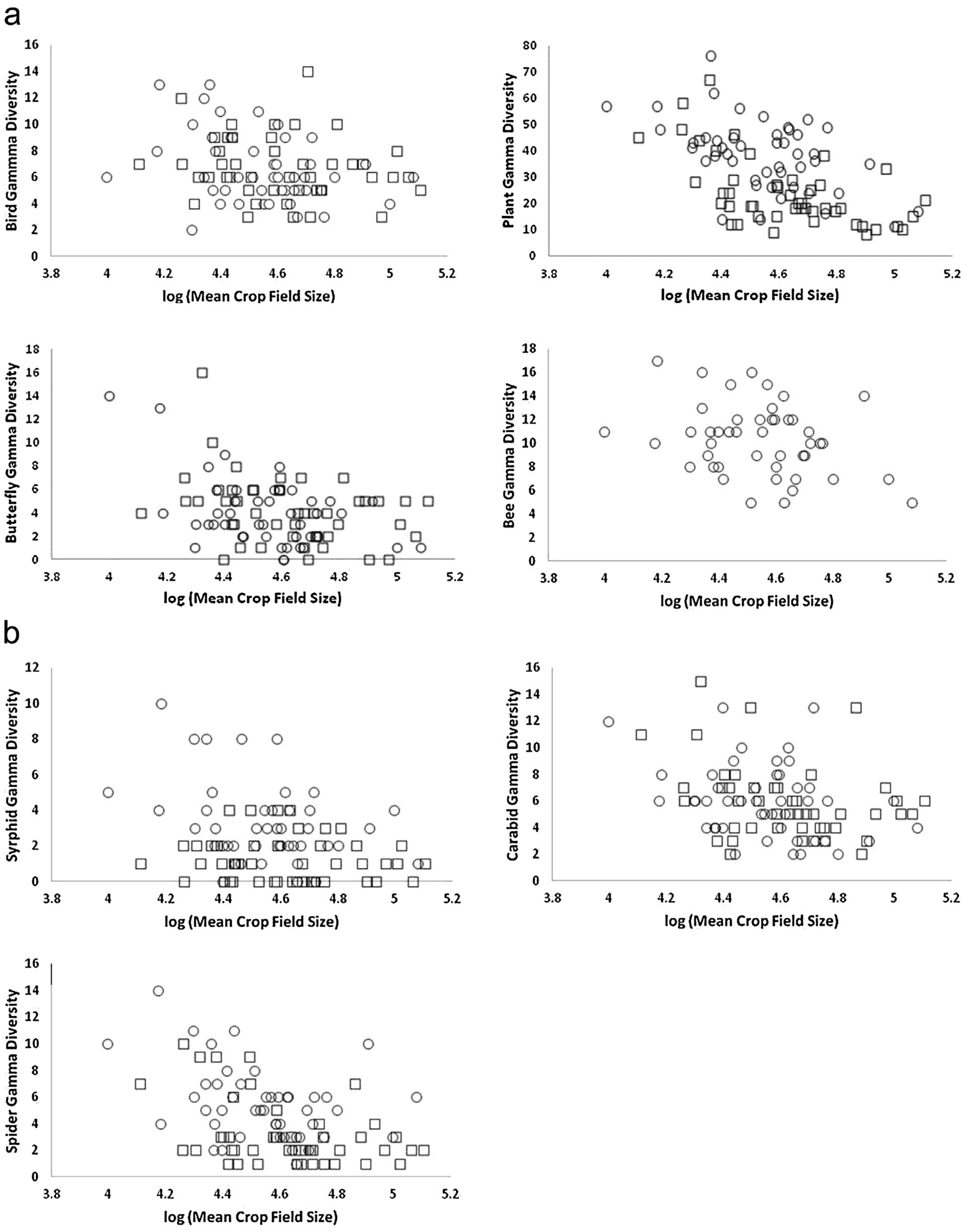

Fig. 4. Relationships between gamma diversity in farmland and log (mean crop field size) for seven taxa; circles are landscapes sampled in 2011 and squares are landscapes sampled in 2012.

therefore a relatively coarse index of the biodiversity within the farmland of each landscape. The fact that we observed a consistent negative effect of mean field size despite the coarseness of our biodiversity measures suggests the result represents a real phenomenon.

We found little evidence that farmlands with higher crop diversity have higher biodiversity. This is in contrast to an empirical study showing that agri-environmental policies aimed at increasing crop diversity in southern Iowa can provide a conservation benefit to birds (Lindsay et al., 2013). It is also in

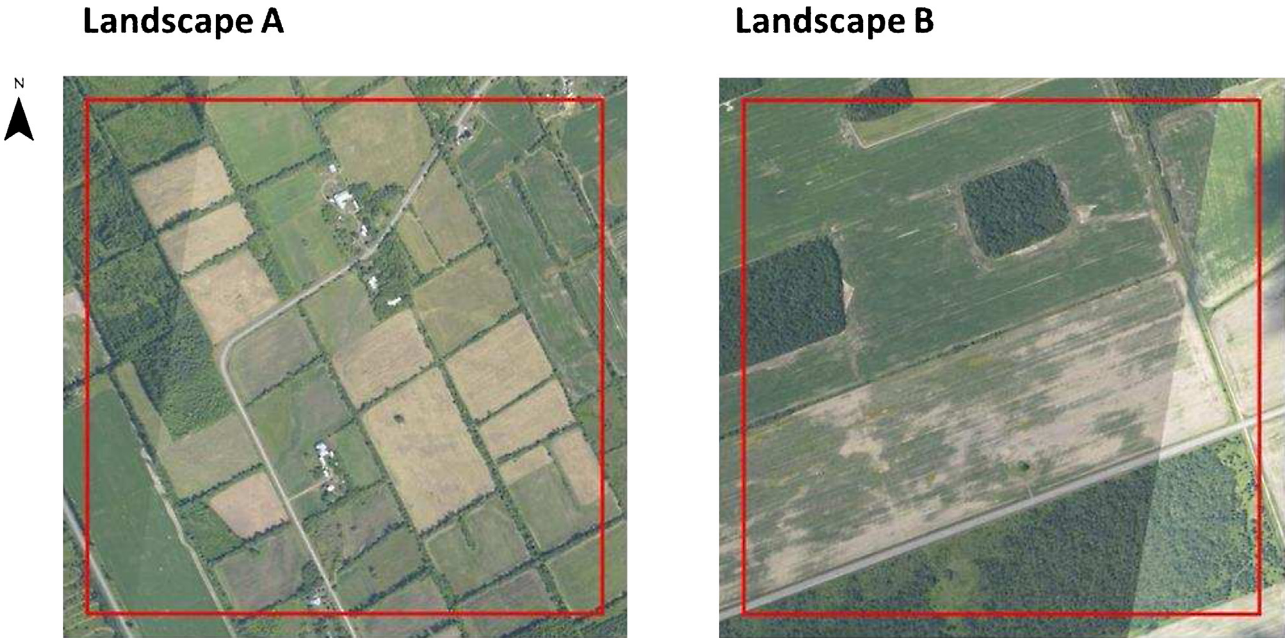

Fig. 5. Two example landscapes containing approximately the same total area of natural and semi-natural covers. Landscape A has small crop fields and most natural and semi-natural cover is in field edges. Landscape B has large crop fields and most natural and semi-natural cover is in forest patches.

apparent contrast to Firbank et al. (2008) who showed a positive relationship between bird diversity and crop diversity across Britain. However, since Firbank et al. did not control for mean crop field size, their result could be due to an effect of mean field size rather than crop diversity, if the two are negatively correlated. Our result is consistent with a meta-analysis of species diversity *vs.* habitat heterogeneity on sets of islands, where habitat heterogeneity was indexed by island elevation range (Allouche et al., 2012); nearly half (47%) of the 43 datasets in that study showed no effect of habitat heterogeneity on biodiversity. However, 33% of the datasets showed peaked biodiversity–heterogeneity relationships, leading the authors to suggest that many of the non-significant relationships were actually peaked relationships where statistical power was too low to detect the curve. This does not appear to be the case in our study, as scatter plots of our biodiversity measures *vs.* crop diversity do not indicate peaked relationships (plots not shown). We suspect that the weak to nonexistent effect of crop diversity in our study could be due to low variation in crop diversity across our region. In our region, the number of crop types is relatively low (4 main crops), and most landscapes contain at least some cover of most crops. Therefore, to produce a range in values of Shannon crop diversity across sample landscapes, we selected landscapes varying in evenness in areal representation of the different crops. Farmlands with low Shannon crop diversity contained mainly a single crop type and farmlands with high Shannon crop diversity contained similar proportions of the major crops. It is possible that the influence of crop diversity on biodiversity would be stronger in agricultural regions containing a wider range of crop types, *e.g.* where highly diverse farmlands contain various types of vegetable crops, grains, and tree crops. Studies in regions with higher crop diversity are needed to test the degree of generality of our results.

Some of our results may be contingent on the particular landscape spatial extent we selected. For example, it is possible that the effects of crop diversity would be manifest at spatial extents larger than the 1 km^2 landscapes we studied. Krawchuk and Taylor (2003) and Smith et al. (2011) found that for some insects and birds (respectively), the relative effects of landscape composition and configuration change with the spatial extent of the landscape considered. We plan to investigate the potential effects of spatial extent in future work.

Although we had predicted a negative effect of mean crop field size, we had not anticipated that it would show the strongest overall effects, relative to the other landscape variables. On the other hand, we note that a negative effect of mean field size is consistent with some recent findings. Lindsay et al. (2013) found a 19% decrease in farmland bird species richness on both organic and nonorganic farms, with an order of magnitude increase in field size. Flick et al. (2012), found a positive effect of patch density (*i.e.* declining mean patch size), measured over the whole landscape (not just in farmland) on butterfly species richness. González-Estébanez et al. (2011) found higher butterfly diversity in Mediterranean landscapes with smaller mean field sizes. Concepción et al. (2012a,b) found that the length of “semi-natural boundaries” in a landscape was generally a stronger predictor than the amount of semi-natural area in the landscape on diversity of a range of taxa in crop fields. Gavish et al. (2012) found higher spider diversity in more fragmented landscapes; they suggested that higher fragmentation enhanced dispersal. Pickett and Siriwardena (2011) found positive effects of configurational landscape heterogeneity on most bird species in agricultural landscapes. Finally, Gaba et al. (2010) found that herbaceous plant diversity in wheat fields was more strongly related to mean field size in the surrounding landscapes (negative relationship) than to landscape composition variables.

While our results suggest an overall negative effect of crop field size on farmland biodiversity, some measures for some taxa showed a stronger effect of proportion of the landscape in crops (positive and negative effects). A notable case is birds, for which the negative effect of percent of landscape in crops is stronger than the negative effect of mean field size. As discussed above, different taxa often respond differently to landscape variables, including variables representing agricultural intensity (*e.g.* Flore et al., 2011;

McMahon et al., 2012). This implies that policies and guidelines for biodiversity in farmland should not be based on a single flagship species group such as birds.

There are at least two factors that could have confounded our results. First, differences among landscapes in their degree of temporal variability, particularly through crop rotation and mowing of forage crops, may have large effects on biodiversity in crop fields (Aviron et al., 2007). Theoretical studies have shown that temporal variation in landscape pattern can more strongly affect population dynamics than the spatial pattern itself (Fahrig, 1992; Keymer et al., 2000; Matlack and Leu, 2007; Hodgson et al., 2009; but see Xu et al., 2006). If landscapes with small crop fields have lower temporal variability than those with large crop fields, this could confound our results. *A priori* we do not expect this is true, but unfortunately we do not currently have a time series of landscape pattern information for our landscapes, from which we could estimate landscape temporal variability. Secondly, if there are strong correlations between our landscape variables and agri-chemical application across our landscapes, our conclusions could also be confounded by their effects. Determining whether such correlations exist will be difficult due to the difficulty of obtaining information on agri-chemical application at a relevant spatial resolution, in our region. We hope to address both the question of landscape temporal variability and the effects of agri-chemicals in future research.

The most compelling applied implication of this study is that policies and guidelines aimed at reducing crop field sizes should be effective in increasing biodiversity within crop fields. Of course, reducing field sizes is easier said than done. For example, along with the trend towards increasing field sizes, many farmers have invested in farm machinery that is tailored to larger fields, despite limited gains in efficiency (Rodríguez and Wiegand, 2009). However, we suggest that reducing field size is likely more practical than increasing crop type diversity. While reverting to smaller crop fields would entail a cost, it would not entail the expense associated with crop diversification if farm profits are maximized by growing the few, most profitable crops. Therefore, if biodiversity conservation within crop fields is a priority, our results suggest that policies and guidelines aimed at reducing crop field sizes should be considered.

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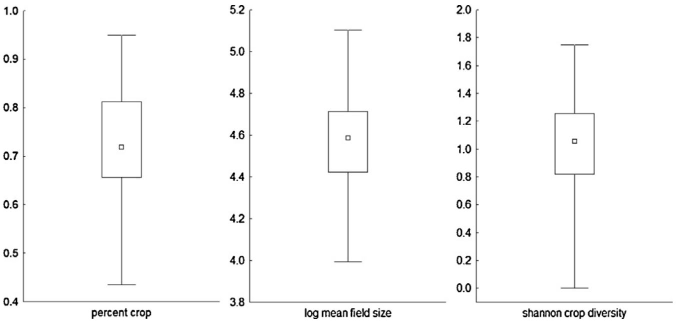
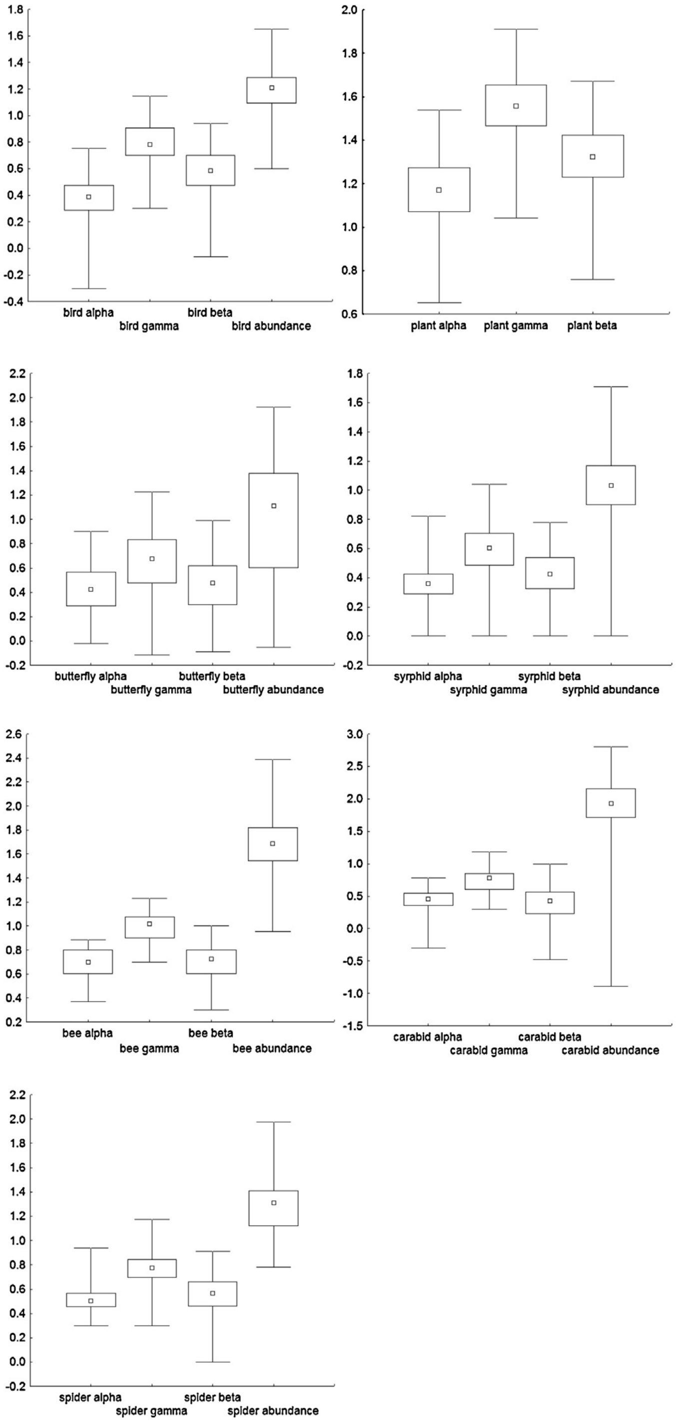
Appendix 1.

Box-and-whisker plots of all predictor and response variables. Response variables are log + 1-transformed. The central point indicates the mean, the box shows the upper and lower quartiles, and the whiskers are the range (minimum and maximum values) of the data.

Predictor variables.



Response variables (log + 1-transformed).



Appendix 2.

List of all taxa found in the biodiversity surveys.

Birds

Common name	Scientific name
Alder flycatcher	*Empidonax alnorum*
American crow	*Corvus brachyrhynchos*
American goldfinch	*Spinus tristis*
American robin	*Turdus migratorius*
Baltimore oriole	*Icterus galbula*
Bank swallow	*Riparia riparia*
Barn swallow	*Hirundo rustica*
Black-capped chickadee	*Poecile atricapillus*
Blue jay	*Cyanocitta cristata*
Bobolink	*Dolichonyx oryzivorus*
Brown thrasher	*Toxostoma rufum*
Brown-headed cowbird	*Molothrus ater*
Cedar waxwing	*Bombycilla cedrorum*
Chipping sparrow	*Spizella passerina*
Common grackle	*Quiscalus quiscula*
Common raven	*Corvus corax*
Common yellowthroat	*Geothlypis trichas*
Cooper's hawk	*Accipiter cooperii*
Eastern kingbird	*Tyrannus tyrannus*
Eastern meadowlark	*Sturnella magna*
Eastern phoebe	*Sayornis phoebe*
Eastern wood-pewee	*Contopus virens*
European starling	*Sturnus vulgaris*
Great crested flycatcher	*Myiarchus crinitus*
Grasshopper sparrow	*Ammodramus savannarum*
Gray catbird	*Dumetella carolinensis*
Gray partridge	*Perdix perdix*
Hairy woodpecker	*Picoides villosus*
Horned lark	*Eremophila alpestris*
Indigo bunting	*Passerina cyanea*
Killdeer	*Charadrius vociferus*
Mourning dove	*Zenaida macroura*
Northern cardinal	*Cardinalis cardinalis*
Northern flicker	*Colaptes auratus*
Pine siskin	*Spinus pinus*
Red-eyed vireo	*Vireo olivaceus*
Red-winged blackbird	*Agelaius phoeniceus*
Ring-billed gull	*Larus delawarensis*
Rock pigeon	*Columba livia*
Rose-breasted grosbeak	*Pheucticus ludovicianus*
Savannah sparrow	*Passerculus sandwichensis*
Short-eared owl	*Asio flammeus*
Song sparrow	*Melospiza melodia*
Spotted sandpiper	*Actitis macularius*
Swamp sparrow	*Melospiza georgiana*
Tree swallow	*Tachycineta bicolor*
Upland sandpiper	*Bartramia longicauda*
Vesper sparrow	*Pooecetes gramineus*
Warbling vireo	*Vireo gilvus*
White-breasted nuthatch	*Sitta carolinensis*
Wilson's snipe	*Gallinago delicata*
Yellow warbler	*Setophaga petechia*

Plants

Common name	Scientific name
Alfalfa	*Medicago sativa*
Alsike clover	*Trifolium hybridum*
Annual blue grass	*Poa annua*
Annual fleabane/daisy fleabane	*Erigeron annuus*
Annual sow-thistle	*Sonchus oleraceus*
Aster spp.	*Asteraceae* spp.
Avens spp.	*Avens* spp.
Awlfruit sedge	*Carex stipata*
Barnyard grass	*Echinochola crusgalli*
Bird rape	*Brassica campestris*
Bird's foot trefoil	*Lotus corniculatus*
Bittersweet nightshade	*Solanum dulcamara*
Black medic	*Medicago lupulina*
Bladder campion	*Silene vulgaris*
Blue-eyed grass	*Sisyrinchium* spp.
Bluegrass sp.	*Poa* spp.
Boneset	*Eupatorium* spp.
Brassicaceae spp.	*Brassicaceae* spp.
Bristly foxtail	*Setaria verticillata*
Brown-eyed susan	*Rudbeckia hirta*
Bull thistle	*Cirsium vulgare*
Canada anemone	*Anemone canadensis*

(*Continued*)

Plants	
Common name	Scientific name
Canada fleabane	*Erigeron canadensis*
Canada goldenrod	*Solidago canadensis*
Canada thistle	*Cirsium arvense*
Chickweed	*Stellaria media*
Chicory	*Cichorium intybus*
Cleavers	*Galium aparine*
Common Burdock	*Arctium minus*
Common milkweed	*Asclepias syriaca*
Common mullein	*Verbascum thapsus*
Common peppergrass	*Lepidium densiflorum*
Common yellow oxalis	*Oxalis stricta*
Corn spurry	*Spergula arvensis*
Crabgrass spp.	*Digitaria* spp.
Creeping buttercup	*Ranunculus repens*
Creeping charlie	*Nepeta hederacea*
Curled dock	*Rumex crispus*
Dandelion	*Taraxacum officinale*
Eastern black nightshade	*Solanum ptycanthum*
Elecampane	*Inula helenium*
Epilobium spp.	*Epilobium* spp.
Evening primrose	*Oenothera biennis*
Fall dandelion/fall hawkbit	*Leontodon autumnalis*
Fall panicum	*Panicum dichotomiflorum*
Fern spp.	*Fern* spp.
Field bindweed	*Convolvulus arvensis*
Field horsetail	*Equisetum arvense*
Galium spp.	*Galium* spp.
Giant foxtail	*Setaria faberii*
Goat's beard	*Tragopogon dubius*
Grass-leaved stitchwort/lesser stitchwort	*Stellaria graminea*
Green foxtail	*Setaria viridis*
Green pigweed	*Amaranthus powellii*
Hairy galinsoga	*Galinsoga ciliata*
Heal-all/selfheal	*Prunella vulgaris*
Inland rush	*Juncus interior*
Jewelweed/spotted touch-me-not	*Impatiens capensis*
Kentucky bluegrass	*Poa pratensis*
Lady's thumb	*Polygonum persicaria*
Lamb's quarters	*Chenopodium album*
Large crab grass	*Digitaria sanguinalis*
Late/giant goldenrod	*Solidago gigantea*
Leafy spurge	*Euphorbia esula*
Lobelia spp.	*Lobelia* spp.
Low cudweed	*Gnaphalium uliginosum*
Marsh bedstraw	*Galium palustre*
Marshpepper smartweed	*Polygonum hydropiper*
Meadow goat's beard/yellow goatsbeard	*Tragopogon pratensis*
Mentha spp.	*Mentha* spp.
Mouse-ear chickweed	*Cerastium vulgatum*
Mouse-eared hawkweed	*Hieracium pilosella*
Mugwort	*Artemisia vulgaris*
Narrow-leaved goldendrod/grass-leaved goldenrod	*Euthamia graminifolia*
New England aster	*Aster novae-angliae*
New York aster	*Symphyotrichum novi-belgii*
Night-flowering catchfly	*Silene noctiflora*
Nodding thistle	*Carduus natans*
Northern marsh yellow cress	*Rorippa palustris*
Oak-leaved goosefoot	*Chenopodium glaucum*
Orchard grass	*Dactylis glomerata*
Ox-eye daisy	*Chrysanthemum leucanthemum*
Panicled aster	*Symphyotrichum lanceolatum*
Perennial rye grass	*Lolium perenne*
Perennial sow-thistle	*Sonchus arvensis*
Philadelphia fleabane	*Erigeron philadelphicus*
Pigweed spp.	*Amaranthaceae*
Pineappleweed	*Matricaria matricarioides*
Plantain	*Plantago major*
Poison ivy	*Rhus radicans*
Polygonum spp.	*Polygonum* spp.
Prickly lettuce	*Lactuca scariola*
Proso millet	*Panicum milliacium*
Prostrate knotweed	*Polygonum aviculare*
Purple loosestrife	*Lythrum salcaria*
Purslane	*Portulaca oleracea*
Purslane speedwell	*Veronica perlgrina*
Quack grass	*Agropyron repens*
Ragweed	*Ambrosia artemisiifolia*
Raspberry	*Rubus idaeus*
Red clover	*Trifolium pratense*
Red fescue	*Festuca rubra*
Redroot pigweed	*Amaranthus retroflexus*
Redtop	*Agrostis gigantea*
Reed canary grass	*Phalaris arundinaceae*
Rough bedstraw	*Galium asprellum*
Rough cinquefoil	*Potentilla norvegica*
Rough fleabane	*Erigeron strigosus*
Rough-stemmed goldenrod	*Solidago rugosa*
Rubia peregrina	*Rubia peregrina*
Sedge spp.	*Carex* spp.
Sensitive fern	*Onoclea sensibilis*
Shepherd's purse	*Capsella bursa-pastoris*
Silvery cinquefoil	*Potentilla argentea*
Slender rush	*Juncus tenuis*
Small sundrops	*Oenothera perennis*
Smartweed spp.	*Polygonaceae* spp.
Smooth bedstraw/wild madder	*Galium mollugo*
Smooth brome	*Bromus inermis*
Smooth crab grass	*Digitaria ischaemum*
Smoothish hawkweed	*Hieracium floribundum*
Soft rush	*Juncus effusus*
Spikerush spp.	*Eleocharis* spp.
Spiny annual sow-thistle	*Sonchus asper*
Spotted joe-pye weed	*Eupatorium maculatum*
Spreading atriplex	*Atriplex patula*
St. john's-wort	*Hypericum perforatum*
Stiff gentian/agueweed	*Gentianella quinquefolia*
Stinging nettle	*Urtica dioica*
Stinking mayweed	*Anthemis cotula*
Stinkweed/field penny-cress	*Thlaspi arvense*
Strawberry	*Fragaria* spp.
Sulphur cinquefoil	*Potentilla recta*
Swamp milkweed	*Asclepias incarnata*
Sweet clover spp.	*Melilotus* spp.
Tall buttercup	*Ranunculus acris*
Tansy	*Tanacetum vulgar*
Three-seeded mercury	*Acalypha rhombides*
Thyme-leaved speedwell	*Veronica serpylliufolia*
Thyme-leaved spurge	*Euphorbia serpyllifolia*
Timothy	*Phleum pratense*
Toadflax/butter-and-eggs	*Linaria vulgaris*
Trifolium spp.	*Trifolium* spp.
Tufted vetch/purple vetch	*Vicia cracca*
Velvetleaf	*Abutilon theophrasti*
Virginia creeper	*Parthenocissus quinquefolia*
Vitis spp.	*Vitis* spp.
Water horehound	*Lycopus americanus*
White campion/white cockle	*Silene latifolia*
White clover	*Trifolium repens*
White sweet clover/white meadowsweet	*Melilotus officinalis alba*
Wild buckwheat	*Polygonum convolvulus*
Wild carrot/queen anne's lace	*Daucus carota*
Wild cucumber	*Echinocystis lobata*
Wild lettuce	*Lactuca virosa*
Wild mint/field mint	*Mentha arvensis*
Wild mustard	*Sinapis arvensis*
Wild parsnip	*Pastinaca sativa*
Wild radish	*Raphanus raphanistrum*
Witch grass	*Panicum capillare*
Wormseed mustard	*Erysimum cheiranthoides*
Yarrow	*Achillea millefolium*
Yellow avens	*Geum aleppicum*
Yellow foxtail	*Setaria glauca*
Yellow hawkweed	*Hieracium caespitosum*
Yellow nut sedge	*Cyperus esculentus*
Yellow rocket/common winter cress	*Barbarea vulgaris*
Yellow sweet clover/yellow meadowsweet	*Melilotus officinalis*

Butterflies	
Common name	Scientific name
American Lady	*Vanessa virginiensis*
Black Swallowtail	*Papilio polyxenes*
Blue spp.	*Polyommatinae* spp.
Bronze copper	*Lycaena hyllus*
Cabbage white	*Pieris rapae*
Clouded sulphur	*Colias philodice*
Common branded skipper	*Hesperia comma laurentina*
Common ringlet	*Coenonympha tullia*
Common wood-nymph	*Cercyonis pegala*
Eastern tailed blue	*Everes comyntas*
European skipper	*Thymelicus lineola*
Eyed brown	*Satyrodes eurydice*
Great spangled fritillary	*Speyeria cybele*
Lady spp.	*Vanessa* spp.
Least skipper	*Ancyloxypha numitor*
Meadow fritillary	*Boloria bellona*
Monarch	*Danaus plexippus*
Mustard white	*Pieris oleracea*
Northern crescent	*Phyciodes cocyta*
Orange sulphur	*Colias eurytheme*
Painted lady	*Vanessa cardui*
Pearl crescent	*Phyciodes tharos*
Pecks skipper	*Polites peckius*
Pink-edged sulphur	*Colias interior*
Question mark	*Polygonia interrogationis*
Red admiral	*Vanessa atalanta*
Skipper spp.	*Hesperiidae* spp.
Spring azure	*Celastrina ladon*
Viceroy	*Limenitis archippus*
White admiral	*Limenitis arthemis*
White spp.	*Pieridae* spp.

Bees
Scientific name
Agapostemon spp.
Andrena asteris
Andrena chromotricha
Andrena commoda
Andrena hitrcincta
Andrena nasonii
Andrena spp.
Andrena wilkella
Apis mellifera
Augochlora spp.
Augochlorella spp.
Bombus bimaculatus
Bombus borealis
Bombus fervidus
Bombus grisecollis
Bombus impatiens
Bombus rufocinctus
Bombus sandersoni
Bombus ternarius
Bombus terricola
Bombus vagans
Chelostoma rapunculi
Chelostoma spp.
Coelioxys spp.
Diadasia spp.
Dialictus spp.
Evylaeus spp.
Halictus confusus
Halictus ligatus
Halictus rubicundus
Halictus spp.
Hoplitis spp.
Hylaeus affinis
Hylaeus annulatus
Hylaeus modestus
Lasioglossum cinctipes
Lasioglossum coriaceum
Lasioglossum leucozonium
Lasioglossum spp.
Lasioglossum truncatum
Lasioglossum zonulum
Megachile brevis
Megachile latimanus
Megachile spp.
Melissodes desponsa
Melissodes druriella
Melissodes illata
Melissodes spp.
Melissodes subillata
Melissodes trinodis
Peponapis pruinosa
Sphecodes cressonii

Syrphids
Scientific name
Allograpta obliqua
Eristalis arbustorum
Eristalis dimidiata
Eristalis tenax
Eupeodes americanus
Eupeodes americanus/pomus
Helophilus fasciatus
Lejops lineatus
Melanostoma mellinum
Paragus spp.
Parhelophilus laetus
Platycheirus hyperboreus
Platycheirus quadratus
Sphaerophoria abbreviata/asymmetrica/philanthus
Sphaerophoria brevipilosa
Sphaerophoria contigua
Sphaerophoria philanthus
Syritta pipiens
Syrphus rectus
Syrphus ribesii
Syrphus vitripennis/rectus
Toxomerus geminatus
Toxomerus marginatus

Carabids
Scientific name
Agonum cupripenne
Agonum gratiosum
Agonum melanarium
Agonum muelleri
Agonum placidum
Agonum thoreyi
Amara aenea
Amara angustatoides
Amara apricaria
Amara lunicollis
Amara otiosa
Amara pallipes
Amara patruelis
Amara rubrica
Anisodactylus rusticus
Anisodactylus sanctaecrucis
Bembidion frontale
Bembidion inaequale
Bembidion mimus
Bembidion obtusa
Bembidion obtusum
Bembidion quadrimaculatum
Biemus discus

(*Continued*)

Carabids
Scientific name
Bradycellus nigriceps
Carabus granulatus
Carabus nemoralis
Chlaenius pusillus
Chlaenius sericeus
Chlaenius tricolor
Cicindela punctualata
Cicindela sexguttata
Clivina fossor
Diplocheila obtusa
Dyschirius montanus
Elaphropus incurvus
Harpalus affinis
Harpalus caliginosus
Harpalus erraticus
Harpalus erythropus
Harpalus herbivagus
Harpalus pensylvanicus
Harpalus pusillus
Harpalus rubripes
Harpalus rufipes
Notiobia terminata
Notiophilus semistriatus
Paratychus proximus
Patrobus longicornis
Poecilus chalcites
Poecilus lepidus
Poecilus lucublandus
Pterostichus caudicalis
Pterostichus commutabilis
Pterostichus melanarius
Pterostichus patruelis
Stenolophus comma
Xestonotus lugubris

Spiders
Scientific name
Agelenopsis potteri
Agelenopsis spp.
Agyneta fabra
Agyneta spp.
Agyneta unimaculata
Allomengea dentisetis
Araneidae spp.
Arctosa emertoni
Arctosa spp.
Argenna obesa
Bathyphantes concolor
Bathyphantes pallidus
Castianeira descripta
Castianeira longipalpa
Clubiona abbotii
Clubiona johnsoni
Coriarachne spp.
Dictyna foliacea
Erigone atra
Euryopis funebris
Glenognatha spp.
Gnaphosa parvula
Gnaphosa spp.
Grammonota gentilis
Halorates plumosus
Islandiana longisetosa
Linyphiidae spp.
Lycosidae spp.
Micaria pulicaria
Microlinyphia pusilla
Misumenops spp.
Neoantistea agilis
Neoantistea spp.
Ozyptila georgiana

(*Continued*)

Spiders
Scientific name
Pachygnatha spp.
Pachygnatha tristriata
Pachygnatha xanthostoma
Pardosa distincta
Pardosa fuscula
Pardosa milvina
Pardosa modica
Pardosa moesta
Pardosa saxatilis
Pardosa spp.
Philodromus cespitum
Pirata aspirans
Pirata insularis
Pirata minutus
Pirata sedentarius
Pirata spp.
Pirata zelotes
Salticidae spp.
Steatoda americana
Talavera minuta
Tennesseellum formicum
Tetragnatha extensa
Tetragnathidae spp.
Thomisidae spp.
Tibellus oblongus
Trochosa ruricola
Trochosa spp.
Walckenaeria fallax
Walckenaeria spp.
Walckenaeria spiralis
Xysticus discursans
Xysticus ferox
Xysticus fervidus
Zelotes fratris
Zelotes spp.

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